



Feeding ecology of Mediterranean common dolphins: The importance of mesopelagic fish in the diet of an endangered subpopulation

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ABSTRACT

The Mediterranean subpopulation of common dolphin (*Delphinus delphis*) is classified as endangered by the IUCN. Still, information about their diet in the Mediterranean is scarce. Stomach contents of 37 common dolphins stranded in the Alboran Sea and Strait of Gibraltar were analyzed. A total of 13,634 individual prey of 28 different taxa were identified. For fish, Myctophidae was the most important family as indicated by the highest index of relative importance (IRI = 8,470), followed by the family Sparidae (IRI = 609). The most important Myctophidae species was Madeira lantern fish (*Ceratoscopelus maderensis*) and for Sparids, the bogue (*Boops boops*). Cephalopods, instead, were found in low quantities only with 31 prey from the Loliginidae, Ommastrephidae, and Sepiolidae families. Overall, our results indicate that common dolphins are mainly piscivorous (99.77%N, 94.59%O, 99.73%W), feeding mostly on mesopelagic prey. Although common dolphins inhabit mainly coastal waters in the study area, the narrow continental shelf seems to facilitate the availability of Myctophids and other members of the mesopelagic assemblage to dolphins when the assemblage migrates to the surface at night. Our results represent the first attempt at quantifying the diet of this predator in the Alboran Sea and Strait of Gibraltar.

Key words: trophic ecology, stomach content analysis, *Delphinus delphis*.

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The short-beaked common dolphin, *Delphinus delphis*, is one of the most abundant cetacean species in European waters (Perrin 2002, Cañadas and Hammond 2008), and once was also abundant and widespread all over the Mediterranean Sea (reviewed in Bearzi *et al.* 2003). However, in the 1970s, due to a dramatic decline in the Mediterranean, this subpopulation was classified as endangered and included in the IUCN Red List of Threatened Species. Currently, common dolphins are still relatively abundant in the Alboran Sea and the Strait of Gibraltar (19.428, 95% CI = 15.277–22.804) dolphins; Cañadas and Hammond 2008), while in the rest of the Mediterranean only sparse sightings of relict groups occur (Bearzi *et al.* 2003). The decline has been attributed to numerous factors, such as habitat degradation, pollution, climate change, and bycatch, but one of the main causes suggested is the reduced availability of their prey due to overfishing (Notarbartolo di Sciara and Gordon 1997, Bearzi *et al.* 2003).

In coastal areas, common dolphins feed mainly on small epipelagic, shoaling fish and some cephalopods (Silva 1999, Santos *et al.* 2004). In contrast, in oceanic areas they feed on species of the deep scattering layer, especially meso- and bathypelagic species, such as myctophids (Brophy *et al.* 2006, Pusineri *et al.* 2007). Traditionally, common dolphins have been considered opportunistic feeders (*i.e.*, with their diet reflecting local prey abundance and availability; *e.g.*, Evans 1994). Recently, it has been proposed that common dolphin display a preference for species with high caloric density (Meynier *et al.* 2008, Spitz *et al.* 2010a). Thus, two foraging strategies, *i.e.*, selective predation (Meynier *et al.* 2008, Spitz *et al.* 2010) and opportunistic feeding (Collet 1981, Santos *et al.* 2013) may coexist in European common dolphins.

Information on the trophic ecology of common dolphins in the Mediterranean Sea is sparse. Here, animals seem to display relatively flexible feeding habits, with epipelagic and mesopelagic fish as preferred prey, but also with the consumption of some eurybathic cephalopod and crustacean species. European anchovy (*Engraulis encrasicolus*), European sardine (*Sardina pilchardus*), round sardinella (*Sardinella aurita*), and garpique (*Belone belone*) have been identified as main prey (Orsi Relini and Relini 1993, Boutiba and Abdelghani 1995, Cañadas and Sagarminaga 1996, Bearzi *et al.* 2003). It has been suggested that the striped dolphin (*Stenella coeruleoalba*) currently occupies the ecological niche of the common dolphin in almost all the Mediterranean Sea (Viale 1985), except in the Alboran Sea and some relict areas (Bearzi *et al.* 2003). Indeed, recent studies showed that the replacement hypothesis seems plausible because their isotopic niches are very similar and their habitats are contiguous (Giménez *et al.* 2017). These studies suggested that this replacement may have occurred if conditions favoring striped dolphins but unfavorable for common dolphins became prevalent, as seen for other small cetaceans (Shane 1994, Kenney *et al.* 1996, Jefferson and Schiro 1997, Palka *et al.* 1997). Nevertheless, these authors highlight the fact that isotopic similarity is not always the result of trophic overlap, since the two dolphins species may be consuming different prey types with similar isotopic compositions, highlighting the need for both types of studies (*i.e.*, isotopic studies and stomach content analyses) to clarify the potential overlap in diet and prey sizes between these two dolphin species.

The present study aims to provide the first quantitative analysis of stomach contents of common dolphins in their main area of distribution in the Mediterranean Sea (Alboran Sea and Strait of Gibraltar). Stomach content analyses provide dietary information with high taxonomical resolution compared with other techniques and the opportunity to infer the size spectrum of the prey eaten (Santos *et al.* 2013). Here, we present data on the overall diet composition and quantify the importance of different

prey species, and examine dietary variability in relation to dolphin size, year, sex, and day of the year. This information is needed to understand the trophic role of this endangered subpopulation.

METHODS

Stomach Content Collection and Characterization of Stranded Dolphins

Stomach contents of common dolphins were collected from stranded animals in the Strait of Gibraltar and the Alboran Sea (Fig. 1). Personnel of the stranding monitoring program coordinated by the regional government of Andalucía (southern Spain) were responsible for the examination of cetacean carcasses and the collection of samples. The program is run by experienced personnel from CEGMA (Centro de Gestión del Medio Marino Andaluz) and CREMA (Centro de Recuperación de Especies Marinas Amenazadas). Full necropsies were carried out whenever the condition of the animal allowed it (fresh to mildly decomposed animals), to establish health status and determine the cause of death. Otherwise, only basic information (*e.g.*, sex, total length, decomposition state) and a few samples were collected (*e.g.*, muscle, teeth, skin, blubber, stomach contents) for further analysis. The whole stomach was collected and frozen for later examination at the laboratory. Stomachs were thawed and washed through a series of sieves of decreasing mesh diameter (1,000 μm \rightarrow 500 μm \rightarrow 300 μm) in order to separate, and retain, hard parts from the soft prey flesh. Cephalopod mandibles (beaks) were preserved in 70% ethanol, while fish otoliths and bones were stored dry. To characterize the sample of dolphins used in our study, we calculated the percentage of adult common dolphins. Due to the lack of studies on maturity at age/length of the Mediterranean common dolphin subpopulation, we used data from animals stranded and bycaught in the northeast Atlantic and Black Sea (Amaha 1994, Murphy and Rogan 2006). These studies indicated that female common dolphins attain sexual maturity at a mean length of about 201 cm and 170 cm, respectively, while for males, maturity was reached at 213 cm and 180 cm,

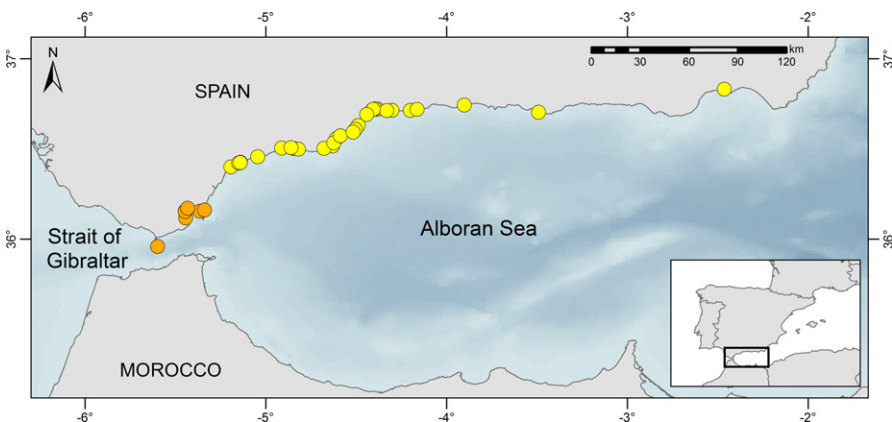


Figure 1. Map of southern Iberian Peninsula showing the stranding location of common dolphin specimens analysed in this study ($n = 37$). Yellow = Alboran Sea samples, orange = Strait of Gibraltar samples.

respectively (Amaha 1994, Murphy and Rogan 2006). Finally, we compared the lengths of male and female dolphins with a *t*-test using the *stats* package in R 3.2.5 (R Core Team 2016).

Stomach Content Analysis

Cephalopod beaks, fish otoliths and bones were identified using published guides (Clarke 1986, Härkönen 1986, Watt *et al.* 1997, Tuset *et al.* 2008, Giménez *et al.* 2016) and the reference collection of the Portuguese Wildlife Society, University of Minho held in the laboratory of Ria Formosa Natural Park in Olhão, Portugal.

The total number of prey was estimated from the number of otoliths or diagnostic bones (*i.e.*, premaxilla, maxilla, cleitrum, dentary, operculum) in the case of fish and mandibles (beaks) in the case of cephalopods, whichever was higher. Otoliths and beaks were measured using a stereomicroscope fitted with a digital camera. Several standard regressions were used to reconstruct fish/cephalopod length and weight (see Table S1). A random subsample of thirty otoliths was measured for each stomach in which a species was present with more than thirty otoliths. Otolith length was usually measured, except for the otoliths of European sardine (*Sardina pilchardus*) and Gobiidae, for which width is the standard measurement (Härkönen 1986). For cephalopod beaks, standard measurements (rostral length for squid and hook length for octopods and sepiolids; Clarke 1986) were taken on either upper or lower beaks. Dorsal mantle length (DML) and body weight of cephalopod prey were also estimated using standard regressions (Clarke 1986). For otoliths/beaks identified only to genus, regressions based on combined data from the species in the group were used when available (Giménez *et al.* 2016). When otoliths were too eroded to allow reliable measurements or when there was no measurable structure available, the mean individual weight for that species in our sample set was used (MIW; *i.e.*, mean of all the estimated weights of a given prey species calculated from the remains in all the stomachs examined; McKinnon 1994, Silva 1999). Each otolith or paired structure was assumed to represent 0.5 fish.

The relative importance of each food item in the diet was quantified using three standard indices: (1) numerical percentage of each prey in relation to the total number of individual prey found in the stomachs (%N); (2) percentage of occurrence of each prey type (%O, *i.e.*, number of stomachs where prey was found divided by the total number of stomachs); and (3) the percentage of total reconstructed prey weight (%W). Additionally, we also used the index of relative importance (IRI, Eq. 1) to measure the overall importance of each prey as a summary index of dietary composition (Hyslop 1980):

$$\text{IRI} = (\%N + \%W) \times \%O \quad (1)$$

Confidence limits for diet composition, taking into account sampling error, were calculated by bootstrapping using the R package *boot* (Canty and Ripley 2016) following Santos *et al.* (2014). The procedure involves the addition of all prey numbers or weights from a sample to the total diet each time a sample is selected. When *n* samples have been taken, numbers or weights for each prey category are calculated and expressed as percentages. One thousand runs were performed and the median and 95% confidence limits were calculated.

The feeding behavior of the species was studied through the construction of the Costello diagram (Costello 1990) modified by Amundsen *et al.* (1996). This

graphical tool has been used to characterize diet variability of cetaceans (Pusineri *et al.* 2007, Romero *et al.* 2012) and other marine predators (Consoli *et al.* 2008, Reisser *et al.* 2013, Varela *et al.* 2016). A scatterplot is built with prey-specific importance for each prey taxon ($\%P_i$; Eq. 2) plotted against the percentage of occurrence ($\%O$). The prey-specific importance metric ($\%P_i$) is defined as the percentage of a prey taxon calculated taking into account only those predators in which the prey taxon actually occurs,

$$\%P_i = \left(\frac{\sum_i W_i}{\sum_{ii} W_{ii}} \right) \times 100 \quad (2)$$

where W_i is the contribution by weight of prey taxa i to the stomach content, W_{ii} is the total stomach content weight in only those predators with prey i in their stomachs. The position of prey types in the two-dimensional plot (see diagram in Fig. 2) provides information on prey importance, feeding strategy and niche width (Amundsen *et al.* 1996). If all prey species display high prey-specific abundance but low occurrence (upper left), the predator population is composed of individual dietary specialists. A population with a generalist dietary strategy would be visualized by all prey types having low prey-specific abundance and moderate to high occurrence (lower right). If prey species are distributed with high prey-specific abundance and high occurrence (upper right), this indicates the predator population specializes on a few dominant species. Prey types with low prey-specific abundance and low occurrence (lower left) are classified as “rare” species. These “rare” species can occur to some degree within any feeding strategy, while numerous points in this position suggest a generalist diet. Furthermore, if all the points are located along or below the diagonal from the upper left to the lower right, the predator population will have a broad niche width (Amundsen *et al.* 1996).

Generalized additive models (GAMs) were used to analyze the effect of several explanatory variables on the numerical importance of the main prey family consumed. A discrete probability distribution was used since the response variable is based on abundance data (*i.e.*, count data). Initial models were fitted using a Poisson distribution. High overdispersion was detected, and therefore models were rerun with a negative binomial distribution with log-link. Dolphin length, year, and day of year were treated as continuous variables and included as smoothers while sex was included as factor. The complexity of smoothers (thin plate regression splines) was constrained by setting a maximum of three degrees of freedom ($k = 4$) to avoid overfitting. To identify the best model a backwards model selection was used, *i.e.*, at each step the least important nonsignificant variable was dropped and the model was rerun until all the remaining explanatory variables showed a significant effect. The effect of removing a nonsignificant variable was tested with an F -test, which confirmed that these variables did not significantly improve the model fit. Obvious patterns in the residuals or highly influential data points, assessed through “hat” values, were checked as recommended by Zuur *et al.* (2007). Although two extreme data points were present in the data set, none of them produced “hat” values exceeding 0.38, and therefore they were not considered as influential and were not dropped from the analysis. Models were fitted using the *mgcv* package (Wood 2004) in R. We also investigated whether the number and the length of prey found in the stomachs varied with dolphin length. Linear models and generalized additive mixed model (GAMM) were fitted to the data, respectively, using the *stats* package (R Core Team 2016) and the

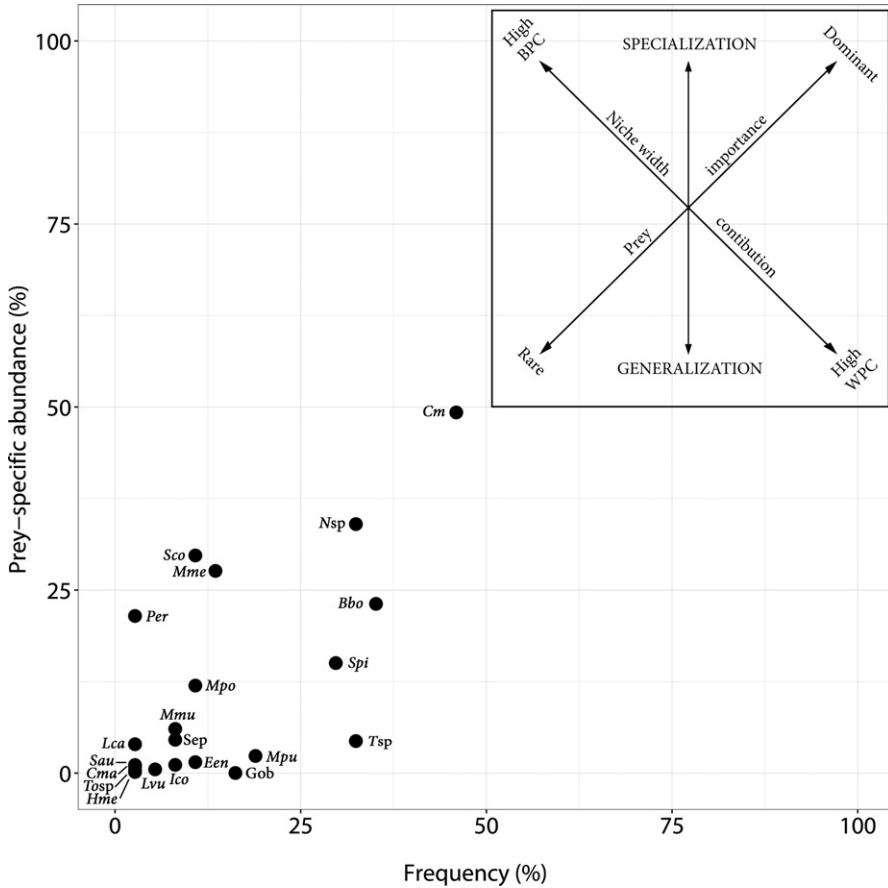


Figure 2. Prey-specific abundance plotted against frequency of occurrence of prey species for common dolphin from the Alboran Sea and Strait of Gibraltar. Explanatory axes for foraging patterns are those of Costello (1990) as modified from Amundsen *et al.* (1996). The two diagonal axes represent the importance of prey (dominant *vs.* rare) and the contribution to the niche width (between-phenotype contribution (BPC) *vs.* within-phenotype contribution (WPC)); the vertical axis defines the predator feeding strategy (specialist *vs.* generalist). *Cm*: *Ceratoscopelus maderensis*; *Nsp*: *Notoscopelus* sp.; *Bbo*: *Boops boops*; *Sco*: *Scomber colias*; *Mme*: *Merluccius merluccius*; *Per*: *Pagellus erythrinus*; *Spi*: *Sardina pilchardus*; *Mpo*: *Micromessistius poutassou*; *Tsp*: *Trachurus* sp.; *Mmu*: *Maurollicus muelleri*; *Sep*: Sepiolidae; *Lca*: *Lepidopus caudatus*; *Sau*: *Sardinella aurita*; *Cma*: *Cepola macrophthalmia*; *Lvu*: *Loligo vulgaris*; *Tosp*: *Todarodes* sp.; *Hme*: *Hoplostethus mediterraneus*; *Een*: *Engraulis encrasicolus*; *Gob*: Gobidae; *Mpu*: *Myctophum punctatum*.

mgcv package (Wood 2004). Results were plotted using the *ggplot2* package (Wickham 2009) in R.

RESULTS

From 2006 to 2014, 37 nonempty stomachs were analyzed: 8 in the Strait of Gibraltar (3 males and 5 females) and 29 in the Alboran Sea (10 males, 17 females,

and 2 individuals of unknown sex; Fig. 1). Dolphin length ranged from 1,130 to 2,030 mm in males and from 1,070 to 2,220 mm in females. No significant differences in length were found between sexes ($t = 0.25$, $df = 27.76$, $P = 0.80$). The percentage of adult specimens in our sample, if we use the NE Atlantic length at maturity, is 5.55% of mature females and no mature males. If we use the estimates obtained for the Black Sea common dolphins, we arrive at a 44.44% of mature females and 30.77% mature males. In general, stomach remains were found in a highly digested condition, with cephalopod beaks and fish bones and otoliths being the most common prey remains found in almost all the stomach analyzed. Some otoliths were too digested to be measured and the MIW was used instead to estimate the weight of individual prey but this took place only in 0.12% of the fish estimated to have been eaten by our sampled dolphins.

In total, we identified 13,634 prey items belonging to 28 different taxa from 18 families, with 93.13% of all prey items identified to at least genus level (Table 1). We identified 144 individuals (1.06%) by using exclusively fish bones. Four species would not have been identified in four different stomachs if bones had not been considered. The average diversity of prey in the stomachs was four species (range 1–11). All data (*i.e.*, Alboran Sea and Strait of Gibraltar samples) were analyzed together since, in addition to the small sample size, there is evidence that common dolphins may be moving between both areas as an important level of gene flow was detected through the Strait of Gibraltar between Alboran Sea and contiguous Atlantic Ocean individuals (Natoli *et al.* 2008).

The diet of common dolphins consisted mainly of fish (99.77%N, 94.59%O, 99.73%W, 18,871.77 IRI), but also include a small amount of cephalopods (0.23%N, 27.03%O, 0.27%W, 13.47 IRI). Myctophidae (86.82%N, 59.46%O, 55.63%W, 8,469.74 IRI) was the most important family, specially the Madeira lantern fish *Ceratoscopelus maderensis* and *Notoscopelus* sp., followed by the family Sparidae (0.78%N, 35.14%O, 16.55%W, 608.84 IRI), particularly bogue (*Boops boops*) and the family Clupeidae (0.76%N, 32.43%O, 9.40%W, 329.24 IRI), with European sardine as the main species of this family (Table 1).

The Amundsen plot (Fig. 2) suggests that common dolphins in the Alboran Sea and the Strait of Gibraltar display a mixed diet. This is in accordance with a generalist strategy, but with two high predominant prey, *i.e.*, Madeira lantern fish and *Nosotocopus* sp. These two species have 49.26% and 34.02% prey-specific abundance, respectively, and the highest percentages of occurrence. Besides these prey, the Amundsen graph highlights the bogue (>23%P and >35%O), the European sardine, and the mackerel (>29%O), and the Atlantic chub mackerel (*Scomber colias*), the European hake (*Merluccius merluccius*), and the common Pandora (*Pagellus erythrinus*) (>21% P) as secondary important prey. Other species were not abundant when present, reflecting that they were not frequently preyed upon.

Prey length distribution presented two differentiated peaks at approximately 50 and 180 mm (Fig. S1) that were similar for both sexes. The smaller group is composed mainly of mesopelagic species (*e.g.*, Madeira lantern fish and *Nosotocopus* sp.), while the second group is characterized mainly of epipelagic species (*e.g.*, European sardine and European anchovy; Fig. S2). Dolphin length was related to prey diversity consumed ($R^2 = 0.36$, $P \ll 0.01$; Fig. 3a) and prey length, but with very small explained deviance ($R^2 = 0.02$, $P = 0.02$; Fig. 3b). Nevertheless, few adult dolphins were present in the data set.

The final GAM model for the number of myctophids in common dolphin stomachs explained 54% of the deviance with significant effects of dolphin length ($P <$

Table 1. Diet composition of common dolphins in the Alboran Sea and Strait of Gibraltar (data pooled). N = number of prey, %N = numerical percentage, O = occurrence, %O = percentage of occurrence, W = prey weight, %W = percentage of reconstructed weight, IRI = index of relative importance. In parentheses are 95% confidence intervals. For explanations on the calculations see main text.

	N	%N	O	%O	W	%W	IRI
Teleosts							
Belonidae							
<i>Belone belone</i>	6	0.04 (0-0.20)	1	2.7 (0-8.11)			
Carangidae							
<i>Trachurus</i> sp.	33	0.24 (0.1-0.78)	12	32.43 (18.92-48.65)	1,588.97	3.6 (1.60-7.13)	124.72 (32.16-384.82)
Cepolidae							
<i>Cepola macrophthalma</i>	1	0.01 (0-0.05)	1	2.7 (0-8.11)	15.89	0.04 (0-0.13)	0.12 (0-1.47)
Cupleidae							
	103	0.76 (0.23-2.45)	12	32.43 (18.92-48.65)	4,143.28	9.4 (2.27-19.67)	329.24 (47.3-1076.14)
<i>Sardina pilchardus</i>	97	0.71 (0.21-2.17)	11	29.73 (16.22-43.24)	4,100.48	9.3 (1.81-20.13)	297.61 (32.76-964.25)
<i>Sardinella aurita</i>	1	0.01 (0-0.04)	1	2.7 (0-8.11)	42.8	0.1 (0-0.32)	0.28 (0-2.92)
Unidentified Cupleidae	5	0.04 (0.01-0.13)	4	10.81 (2.70-21.62)			
Engraulidae							
<i>Engraulis encrasicolus</i>	16	0.12 (0.01-0.64)	4	10.81 (2.70-21.62)	110.71	0.25 (0.04-0.64)	3.98 (1.08-384.82)
Gadidae							
<i>Micromesistius pouassou</i>	114	0.84 (0.02-3.17)	4	10.81 (2.70-21.62)	1,960.41	4.45 (0.09-12.57)	57.1 (0.297-340.29)

(Continued)

Table 1. (Continued)

	N	%N	0	%0	W	%W	IRI
Gobiidae							
Unidentified Gobiidae	15	0.11 (0.02-0.54)	6	16.22 (5.40-29.73)	4.21	0.01 (0-0.03)	1.94 (0.11-16.95)
Macrouridae							
<i>Coelorhynchus caelorhynchus</i>	1	0.01 (0-0.02)	1	2.7 (0-8.11)			
Merlucciidae							
<i>Merluccius merluccius</i>	71	0.52 (0.01-2.18)	5	13.51 (2.70-24.32)	2360.09	5.35 (0.11-17.56)	79.36 (0.324-480.08)
Myctophidae							
11837	11837	86.82 (65.18-95.72)	22	59.46 (43.24-72.97)	24,528.7	55.63 (26.36-72.98)	8469.74 (3,958.19-12,310.04)
<i>Benitosema glaciale</i>	56	0.41 (0-2.25)	1	2.7 (0-8.11)			
<i>Ceratospopelus maderensis</i>	8181	60 (17-86.3)	17	45.95 (29.73-62.16)	13210.67	29.96 (5.65-56.18)	4133.45 (673.38-8,850.86)
<i>Myctophum punctatum</i>	464	3.4 (0.34-8.37)	7	18.92 (5.47-32.43)	588.14	1.33 (0.15-2.92)	89.62 (2.68-366.13)
<i>Notosopelus</i> sp.	2785	20.43 (2.87-49.25)	12	32.43 (18.92-48.65)	10,729.89	24.33 (3.88-47.99)	1451.68 (127.71-4,730.73)
Unidentified Myctophidae	351	2.57 (0.37-10.92)	8	21.62 (8.11-35.14)			
Scombridae							
<i>Scomber colias</i>	26	0.19 (0.01-0.84)	4	10.81 (2.70-21.62)	1,429.29	3.24 (0.13-10.53)	37.1 (0.378-245.82)
Sparidae							
106	106	0.78 (0.26-2.89)	13	35.14 (21.62-51.28)	7,298.38	16.55 (5.85-35.90)	608.84 (132.10-1,989.15)
<i>Boops boops</i>	103	0.76 (0.25-2.82)	13	35.14 (21.62-51.28)	7,040.11	15.97 (5.68-36.49)	587.49 (128.21-2,015.82)

(Continued)

Table 1. (Continued)

	N	%N	O	%O	W	%W	IRI
<i>Pagellus erythrinus</i>	3	0.02 (0-0.14)	1	2.7 (0-8.11)	258.27	0.59 (0-2.44)	1.64 (0-20.92)
Sternoprionidae	716	5.25 (0-19.78)	3	8.11 (0-18.85)	203.85	0.46 (0-1.49)	46.33 (0-400.94)
Trachichthyidae	1	0.01 (0-0.02)	1	2.7 (0-8.11)	11.99	0.03 (0-0.08)	0.09 (0-0.88)
<i>Hoplostethus mediterraneus</i>							
Trichiuridae	5	0.04 (0-0.11)	1	2.7 (0-8.11)	320.55	0.73 (0-2.12)	2.06 (0-18.09)
<i>Lepidopus caudatus</i>							
Unidentified teleost	552	4.05 (0.27-11.9)	18	48.65 (32.43-64.86)			
Total teleosts	13603	99.77 (99.16-99.93)	35	94.59 (86.48-100)	4,3976.32	99.73 (99.46-99.92)	18871.77 (17,176.66-19,985)
Cephalopods	9	0.07 (0.01-0.28)	4	10.81 (2.70-21.62)			
Loliginidae	3	0.02 (0-0.09)	2	5.41 (0-13.51)			
<i>Alloteuthis</i> sp.							
<i>Loligo vulgaris</i>	6	0.04 (0-0.22)	2	5.41 (0-13.51)	28.78	0.07 (0-0.22)	0.59 (0-5.94)
Ommastrephidae	5	0.04 (0.01-0.12)	4	10.81 (2.70-21.62)	68.97	0.16 (0.01-0.33)	2.09 (0.05-9.73)
<i>Illex coindetii</i>	4	0.03 (0-0.12)	3	8.11 (0-18.85)	28.73	0.07 (0-0.27)	0.77 (0-7.35)
<i>Todarodes</i> sp.	1	0.01 (0-0.01)	1	2.7 (0-8.11)	40.23	0.09 (0-0.22)	0.27 (0-1.87)

(Continued)

Table 1. (Continued)

	N	%N	O	%O	W	%W	IRI
Sepioidae	11	0.08 (0.01–0.38)	5	13.51 (2.70–24.32)			
<i>Sepioida atlantica</i>	4	0.03 (0–0.13)	2	5.41 (0–13.51)			
Unidentified Sepioidae	7	0.05 (0–2.24)	3	8.11 (0–18.85)	21.78	0.05 (0–0.19)	0.82 (0–45.81)
Unidentified cephalopod	6	0.04 (0–0.23)	2	5.41 (0–13.51)			
Total cephalopods	31	0.23 (0.07–0.79)	10	27.03 (13.51–40.54)	119.53	0.27 (0.09–0.54)	13.47 (2.16–53.92)

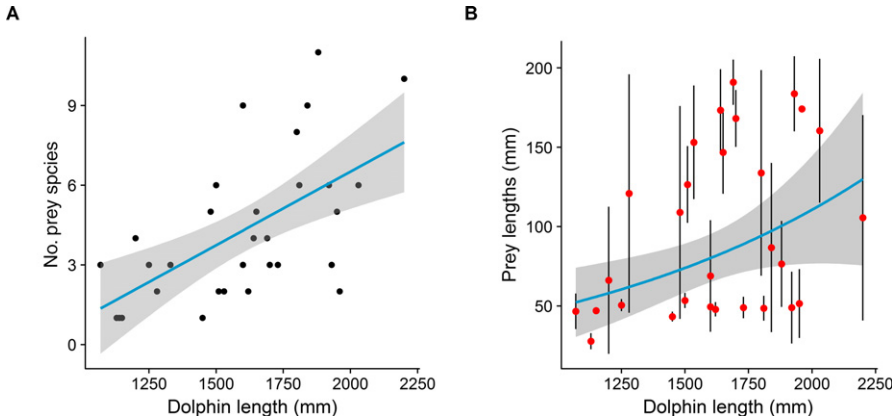


Figure 3. (A) Relationship (blue line) between dolphin length and number of prey species (dots) with 95% confidence interval (shaded area) in the stomach of common dolphins; (B) Relationship between predator length and prey length (blue line) with 95% confidence interval (shaded area). Red dots represent mean length values and standard deviations are depicted with black lines.

0.01) and day of year ($P < 0.01$). Smoothers are represented in Figure 4, and their shape suggests that the numerical importance of myctophids increases with dolphin length and fluctuates through the year. Results indicate a higher consumption of myctophids in summer-early autumn. We cannot extract conclusions on the effect of day of year on common dolphin diet in spring as there are no samples from that period, as it is apparent from the wide confidence limits shown over that period (see Fig. 4).

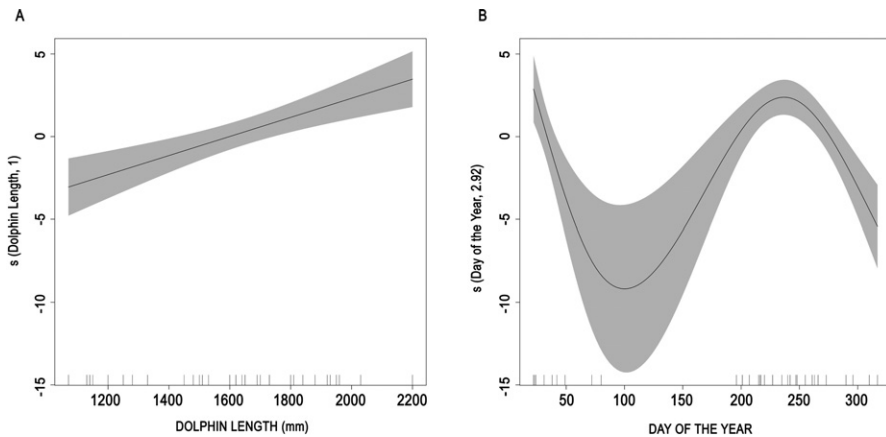


Figure 4. Significant smoothers for the effect of covariates length and day of the year of the GAM fitted over the numerical importance of myctophids in the stomachs of common dolphins. Shaded areas represent the 95% confidence intervals.

DISCUSSION

This study provides the first quantification of the diet, based on stomach content analysis, of common dolphins in their main areas of abundance in the Mediterranean Sea, the Alboran Sea, and Strait of Gibraltar. We highlight the importance of lipid-rich mesopelagic species (particularly Madeira lantern fish and *Nosotospelus* sp.) in the diet of this endangered Mediterranean common dolphin subpopulation.

The importance of mesopelagic, energy-rich prey (Spitz *et al.* 2010*b*) in the common dolphins diet has also been reported in oceanic waters in other European regions (*e.g.*, Brophy *et al.* 2006, Pusineri *et al.* 2007, Meynier *et al.* 2008). However, common dolphins in our study area are distributed near the coast (Cañadas and Hammond 2008, de Stephanis *et al.* 2008). In the Alboran Sea, a bimodal pattern in common dolphin abundance is observed, with high densities found around the shelf edge (~150–200 m depth), with a second peak in abundance in deep waters (~1,000 m depth), that are close to the coast due to the narrow continental shelf in the region (Cañadas and Hammond 2008). In the Strait of Gibraltar, instead, they are mainly associated with deep waters along the northern edge of the channel (de Stephanis *et al.* 2008). Our results highlight the importance of mesopelagic fish in the diet of common dolphins in the Alboran Sea and Strait of Gibraltar. This information is novel, as epipelagic prey were thought to be the most important prey in Mediterranean common dolphins' diet (Bearzi *et al.* 2003), although it also agrees with the most recent published data from North Aegean Sea, where mesopelagic fish were also considered important prey items in common dolphins' diet (Milani *et al.* 2016). In our dolphins' stomach content sample, in addition to mesopelagic prey, we found coastal species such as European sardine, which would indicate that common dolphins are generalist predators in the Alboran Sea and Strait of Gibraltar. Observations of common dolphin feeding behavior registered on board by Cañadas and Hammond (2008), who detected feeding events of round sardinella, European sardine, and garfish, reinforce our conclusions.

We hypothesize that the epipelagic species found in stomach contents may be consumed during daylight hours, when these prey are located over the continental shelf and the shelf break. Otherwise, mesopelagic prey may be consumed during nighttime, when these prey migrate to the surface from the deep scattering layer. In general, mesopelagic species can be found at night from the surface to 250 m depth, while, during the day, they are found in deeper waters (>800 m) (Hulley 1984). The presence of deep waters very close to the coast in our study area due to the narrow shelf, would allow dolphins to access both types of prey. Common dolphin's diving capability is believed to be limited to shallow waters with regular dives normally only down to 50 m (Evans 1975, 1982, 1994). Hence, the capture of mesopelagic species during the daylight would potentially push common dolphins closer to their physiological limits.

Myctophids were firstly studied in the Mediterranean Sea in the 1900s (Taning 1918, Jespersen and Taning 1926, Goodyear *et al.* 1972), and recently new studies have provided information on their feeding ecology, vertical distribution and diversity in the western Mediterranean Sea (Olivar *et al.* 2012, Valls *et al.* 2014, Bernal *et al.* 2015). The Mediterranean contains less diversity in myctophid species than the adjacent North Atlantic Ocean (Goodyear *et al.* 1972, Hulley 1984, Olivar *et al.* 2012), but these fish still play an important role in this marine area (Olivar *et al.* 2012). Overall, myctophids are a key component of open-ocean food webs (Davison *et al.* 2013, Valls *et al.* 2014) due to their abundance and to the role they play in the

energy flow between different trophic levels (Valls *et al.* 2014) being the prey of a wide range of predators worldwide (Cherel *et al.* 1993, Fanelli *et al.* 2009, Pereira *et al.* 2011, Anastasopoulou *et al.* 2013).

In this study, the consumed prey diversity increased with dolphin length, although our model explained a small amount of deviance. This increase could take place because older dolphins have become more experienced in prey capture and/or can access more prey types due to higher swimming capabilities. Our results also indicate that common dolphins seem to increase their intake of myctophids as they grow, a fact that may be related again to the improvement of diving capabilities of older individuals, that facilitates access to deeper waters, an improved foraging behavior capacity of adult common dolphins also mentioned by Silva (1999). Further analyses including greater number of mature, older dolphins are needed to confirm these relationships and to be able to make a broad generalization for the whole population.

In our study, a poor relationship was found between prey length and dolphin length. The low explained deviance could be, in part, due to the low percentage of adults in our data set, although greater sample sizes in other studies did not find any relationship neither, leading the authors to conclude that prey size is of secondary importance in marine mammal feeding strategies within certain prey size ranges (MacLeod *et al.* 2006, Meynier *et al.* 2008, Spitz *et al.* 2014). Although finding a poor relationship between prey and dolphin length, the presence of a bimodal prey size distribution in the stomach analyzed in this study suggests that common dolphins could be preferentially selecting small, supposedly abundant, and energy rich species, but also some bigger species, such as European hake or bogue. Common dolphins predate with a pincer movement of the jaws, supported by a row of small, peg-like teeth, which allow the piercing, gripping, and handling of the prey (MacLeod 1998). Both behavior and morphology present equal efficiency to capture both relatively small and large prey (MacLeod *et al.* 2006). No significant differences between sexes were found in the diet in accordance with the results from stable isotope data (Giménez *et al.* 2017).

There are currently no estimates of myctophid abundance in the study area, mainly because this species has no commercial interest, and also because the research surveys in the region do not sample the open waters. In our sample, myctophid consumption seems to fluctuate in a seasonal pattern, which could be related to a different availability throughout the year. If common dolphins are feeding opportunistically, they could take advantage of the available myctophids ascending at night to the near-surface, when other prey are less available; alternatively, they could be selecting energy-rich species over other available prey. Only detailed information of prey availability and abundance at the appropriate temporal and spatial scales will allow us to determine the feeding strategy of the common dolphin in the Mediterranean Sea.

Diet overlap analysis, especially with striped dolphins, could be confirmed if the isotopic overlap found in stable isotope signatures (Giménez *et al.* 2017) is an indication of similar diets. There are drawbacks in describing the feeding habits of a population by the analysis of stomach content of stranded animals (*e.g.*, da Silva and Neilson 1985, Jobling and Breiby 1986, Pierce and Boyle 1991), since a possible bias could arise by having an overrepresentation in the sample of sick, injured animals that perhaps were not feeding normally, or results could be biased due to a predominance of animals in the sample that were feeding near the coast prior to the stranding (Pierce and Boyle 1991). The need to be aware of other sources of bias, such as secondary ingestion (remains present in the stomach could originate from the diet of the preyed fish; see Pierce *et al.* 2007) or differential digestion rate between prey types

(Pierce and Boyle 1991), have also been discussed. Nevertheless, recent studies have validated the utility of stomach content analysis, as being representative of the diet of healthy free-ranging individuals (Dunsha *et al.* 2013) and of the size spectrum of the prey eaten (Santos *et al.* 2013). This detailed diet information is the first step to assess the role of common dolphins in this marine ecosystem. Future studies must focus on the assessment of the consumption rates of this species in the area to be able to evaluate the degree of overlap with local fisheries and inform future sound management measures for the conservation of this endangered subpopulation. Nevertheless, more adult specimens should be analyzed to generalize the present results to the whole common dolphin population. Moreover, further research efforts must be allocated to estimate the abundance and distribution of mesopelagic fish in the Alboran Sea and the Strait of Gibraltar. Ultimately, this information can be used for management purposes by building an ecosystem model and testing the effect of different fishing policies for the study area.

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SUPPORTING INFORMATION

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Figure S1. Estimated fish length for all prey species found in the stomach of common dolphins. The probability density function of length is also represented together with the mean value (dashed line). Male = orange, Female = gray.

Figure S2. Estimated fish length for the main prey species found in the stomach of common dolphins. The probability density function of length is also represented together with the mean value (dashed line).

Table S1. Regression equations used to estimate fish and cephalopod sizes: L, total length (mm) for fish and dorsal mantle length (mm) for cephalopods; W, total weight (g); OL, Otolith length (mm); OW, otolith width (mm); LHL, lower hood length (mm); LRL, lower rostral length (mm).